

de cette activité. L'olfaction ne semble pas intervenir dans la localisation du nid pendant la période étudiée ici (YAHN et al. 1983), et ce n'est qu'après l'ouverture des yeux que les performances des jeunes dans les grandes cages s'améliorent.

Les performances de ramassage des jeunes et de leur retour spontané que nous avons observées dans les longues cages sont exactement inversement corrélées. Il existe donc une concordance entre le comportement de ramassage de la femelle et l'inaptitude des jeunes à rentrer au nid. Ceci est confirmé par l'observation d'une persistance du comportement de ramassage de la femelle pendant une période allant jusqu'à 48 jours, lorsque les jeunes d'une femelle sont remplacés périodiquement par d'autres jeunes plus immatures (POUR-TIER L., comm. pers.).

L'inaptitude des jeunes pour le retour spontané dans un type d'environnement relativement complexe constitue un handicap vis à vis des chances de survie, dans un environnement naturel. Celui-ci est contre-balancé par le plus fort taux de ramassage des femelles dans cette situation. Ces expériences montrent le caractère adaptatif du comportement de la femelle, dont l'expression différentielle, en fonction des caractéristiques de l'espace, peut se révéler d'une considérable valeur pour la survie des jeunes.

Résumé

Les auteurs ont testé les performances de ramassage des jeunes dans deux groupes composés chacun de dix Gerbilles de Mongolie femelles adultes ainsi que celles de retour spontané au nid de leurs jeunes, dans deux environnements expérimentaux différents, de la parturition au sevrage. Le premier environnement consistait en une très longue cage (120 × 15 cm), munie d'une boîte nichoir. Le second était une cage standard, carrée (40 × 40 cm), avec un nid ouvert. Les latences du premier contact femelle-jeune durant les tests ne diffèrent pas significativement. Le taux de ramassage des jeunes est plus élevé entre les jours 6 et 18 *post-partum* pour les animaux des longues cages que pour ceux des cages standard. De forts taux de ramassage sont observés pendant une plus longue période dans les longues cages que dans les cages standard. L'inverse est observé en ce qui concerne le retour spontané des jeunes au nid, qui fait son apparition au dixième jour dans les longues cages et au deuxième jour dans les cages standard. Ces différences comportementales sont rapportées aux différences de structures des deux environnements expérimentaux accessibles aux animaux, permettant de distinguer une zone «favorable à l'élevage des jeunes» et une zone «non favorable à l'élevage des jeunes». Ce protocole a permis de montrer les possibilités d'adaptation du comportement de la femelle adulte à la structuration particulière de son environnement, ce qui, dans un environnement naturel est décisif pour la survie des jeunes.

Zusammenfassung

Raumnutzung und Rückkehr zum Nest bei der Mongolischen Rennmaus (Meriones unguiculatus)

Geprüft wurde in zwei verschiedenen Käfigtypen an je 10 Weibchen von *Meriones unguiculatus*, mit welcher Intensität sie ihre Jungen im Alter von 1–19 Tagen ins Nest trugen und wie weit die Jungen aktiv zum Nest zurückkehrten. Käfig A war gestreckt (120 × 15 cm) und enthielt einen geschlossenen Nestkasten. Käfig B war quadratisch und mit einem offenen Nest ausgestattet.

In Käfig A wurden die Jungen intensiver eingetragen als in Käfig B. Dafür kehrten in Käfig B die jungen häufiger aktiv ins Nest zurück als in Käfig A. Diese Unterschiede können damit erklärt werden, daß Käfigtyp A deutlicher in eine Nest- und eine Außenregion gegliedert war und die Jungen bei Orientierung an der Käfigwand mit dem Tastsinn in Käfig B eher zufällig auf das Nest stießen als in Käfig A.

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The effect of fire on the small mammal community in Hluhluwe Game Reserve

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Abstract

Investigated was the effect of fire on small mammals. Four permanent trapping grids in *Acacia* savanna, subjected to various burning treatments, were monitored from July 1982 to December 1983. An area not burnt and an area with a patchy-burn showed an increase in rodent densities immediately after the fire. A burning experiment disclosed no animals fleeing from the blaze. Species composition and diversity indexes of the small mammal community were relatively unaffected by the burns. No age-class of *Praomys natalensis* was more vulnerable to the fire than any others. Each sex of *P. natalensis* and *Aethomys chrysophilus* responded similarly to the burns while more *Lemniscomys griselda* females were captured in post-burn trapping. An effect of burning was that cleanly burnt areas seemed to stimulate reproduction; relatively more *P. natalensis* adult came into reproductive condition during spring in these areas. The mean distance between captures (range distance) of *P. natalensis* fluctuated inversely with changes in population densities. The mobility of *P. natalensis* and *L. griselda* following the burns increased while the survival rates of *P. natalensis*, *A. chrysophilus*, and *L. griselda* appeared greater in unburnt areas. The 1982/83 drought caused the population densities of each species in the small mammal community to "crash".

Introduction

In recognition of the vital role fire plays in natural ecosystems, its use has now been accepted as a necessary tool in land management (EDWARDS 1984). The burning programme employed at Hluhluwe Game Reserve (HGR) has two major objectives, to combat bush encroachment; and to maintain the fire-climax grasslands (unpubl. NATAL PARKS BOARD report).

In order to maintain a rich and diverse rodent community correct grassland management in natural areas is vital. The immediate responses of small mammals to a blaze vary; animals may flee from the flames (DELANY 1974; SWANEPOEL 1981), or seek refuge in burrows, holes, crevices, or islands of vegetation missed by fire (CHEESEMAN and DELANY 1979; BEGG et al. 1981) while others burn or suffocate (DELANY 1974; CHRISTIAN 1977). CHEESEMAN and DELANY (1979) report rodents moving ahead of the flames (200–300 m), and they suggest the animals respond to a warning stimulus (noise of combustion, smell of/or smoke) other than the heat of the fire itself. Several authors report direct mortality as being negligible because of high post-burn survival (DELANY 1974; BEGG et al. 1981; SWANEPOEL 1981).

Small mammal habitat is severely and abruptly modified by fire in that food supply is reduced and cover removed. Post-burn numbers decline due to hunger and enhanced predation (BEGG et al. 1981; SWANEPOEL 1981; ROWE-ROWE and LOWRY 1982). Reproduction and recruitment can be affected by fire through delayed breeding and reduced litter sizes (BEGG et al. 1981).

The objective of the present study was to investigate the effect of controlled burning on the abundance and diversity of small mammals in HGR.

Study area

HGR ($28^{\circ} 00' - 28^{\circ} 91'S$, $32^{\circ} 00' - 32^{\circ} 09'E$; Fig. 1) covers 23 067 ha; the topography, characterised by a profusion of drainage lines, is extremely rugged with altitude ranging from 90 m to 750 m a.s.l. The mean annual rainfall (averaged over 52 y) is 968 mm with the wettest months occurring between October and March.

The study area falls within the Zululand Thornveld subcategory of the Coastal Tropical Forest Types, and the Lowveld subcategory of the Tropical Bush and Savanna types of ACOCKS (1975). Forest communities are restricted from high rainfall hillsides to riverine belts. Much of the area is covered by savannas dominated by *Acacias*, in particular *A. karroo*, *A. burkei*, *A. nilotica*, *A. tortilis*, *A. gerrardii*, *A. nigrescens*, and *A. caffra*. These generally have grass cover of tall tufted perennials such as *Themeda triandra* and *Cymbopogon* spp. (BROOKS and MACDONALD 1983).

Trapping and vegetation monitoring were conducted primarily in *Acacia* savanna in the study area situated in the northeastern corner of HGR (Fig. 1).

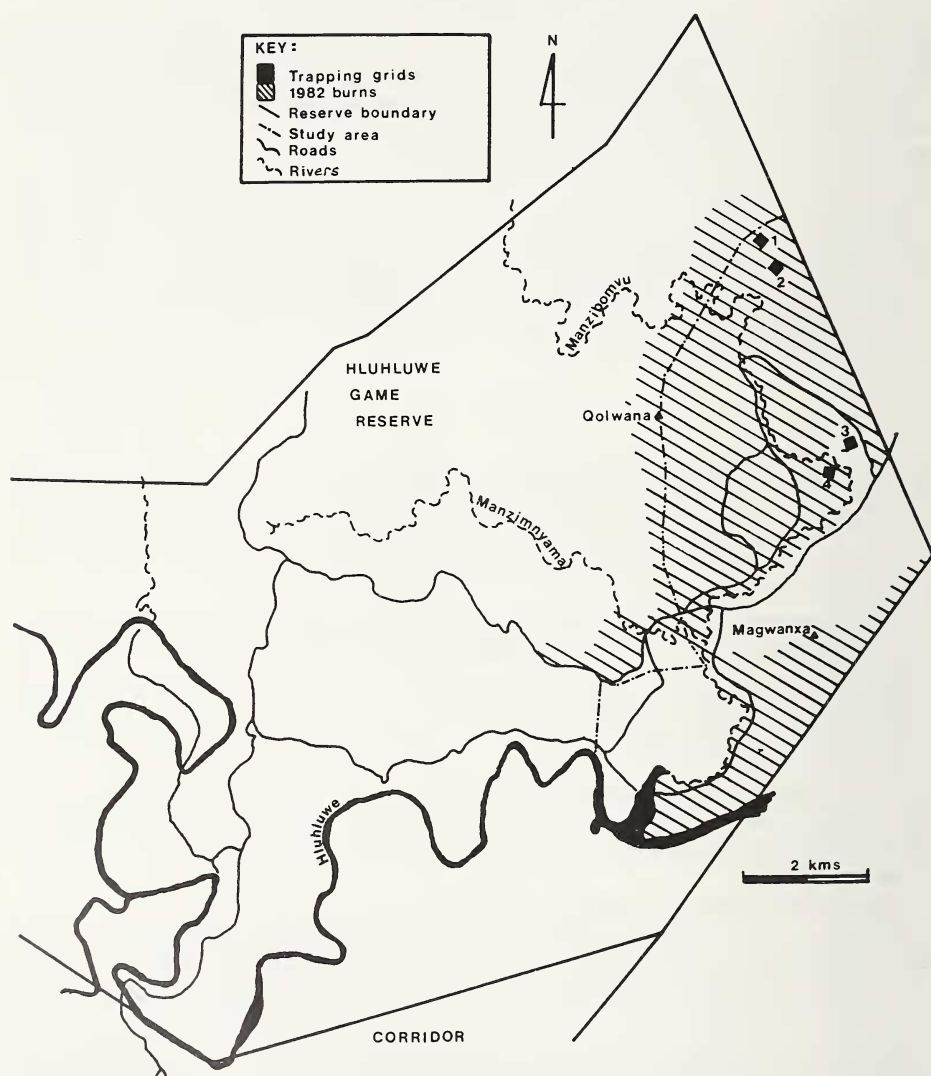


Fig. 1. A map of the 1982 burns in the Hluhluwe Game Reserve study area showing the locations of the trapping grids. 1 = clean-burn 1, 2 = patchy-burn, 3 = no-burn, 4 = clean-burn 2

Materials and methods

Trapping was conducted on 10 × 10 grids with PVC livetraps (WILLAN 1978), set at 15 m intervals. The trap was usually placed in the most likely site within one metre of the trap station; all traps were checked daily in the morning, rebaited, with a mixture of equal parts rolled oats and peanut butter, and reset if necessary.

Captured animals were identified, weighed, and sexed; and capture points on the grid were recorded. The following criteria were used to evaluate reproductive condition: females, the state of the vaginal opening (perforate or imperforate) and the condition of the nipples (small, enlarged, lactating); males, the position of the testes (scrotal or abdominal). Each animal was individually marked using a toe-clip code before release at its capture site.

Animals were assigned to age-classes according to body mass i. e. adult, sub-adult, or juvenile (Table 1). The lower limit of the adult class was calculated by subtracting the standard deviation from the mean weight of the "scrotal" or "perforate adults", to accommodate animals in an emaciated condition caused by the drought. The mean trap distance between captures of individuals was used to assess the range distance of each species.

Table 1. The weight categories used to determine age classes of four rodent species

Species	adult (g)	Females sub-adult (g)	juvenile (g)	adult (g)	Males sub-adult (g)	juvenile (g)
<i>Praomys natalensis</i>	>33	21–33	<21	>31	21–31	<21
<i>Saccostomus campestris</i>	>36	21–36	<21	>41	21–41	<21
<i>Aethomys chrysophilus</i>	>63	31–63	<31	>71	31–71	<31
<i>Lemniscomys griselda</i>	>47	21–47	<21	>64	21–64	<21

Population densities were estimated by a weighted mean mark-recapture formula (BEGON 1979):

$$\hat{N} = \frac{M_i \times n_i}{(\sum m_i + 1)}$$

where \hat{N} = estimate of the population
 M_i = number of marked individuals at risk on day i
 m_i = number of marked individuals caught on day i
 n_i = number of individuals caught on day i

Standard error was calculated with the formula (BEGON 1979):

$$SE = \hat{N} \sqrt{\frac{1}{\sum m_i + 1} + \frac{2}{(\sum m_i + 1)^2} + \frac{6}{(\sum m_i + 1)^3}}$$

Species diversity was calculated using the formula (SHANNON 1948):

$$H = \frac{n \log n - \sum f_i \log f_i}{n}$$

where H = species diversity index, f_i = number of individuals of one species caught during the trapping session, and n = total number of individuals of all species caught during the trapping session (SHANNON 1948). Diversity indexes were compared with the test devised by HUTCHESON (1970).

After extensive exploratory trapping in the study area, four permanent grids were sited in *Acacia* savanna which had not been burnt since 1980. The grids were loosely paired i. e. about 600 m distant, the two pairs were separated by about 3.5 kms (Fig. 1).

Three of the grids were burnt in the first week of August 1982. One had a patchy burn while two had clean burns; the fourth unburnt grid was used as a control. The patchy burn was hot and clean with a mosaic of discrete unburnt islands of the herb layer remaining; these islands varied in area from several to a hundred or more square metres. The clean burns were hot and thorough with no herb layer remaining. In each case the clean-burn grid was adjacent to either the patchy-burn or the no-burn grid. Grids were trapped just before (July) and just after (August) the burns in 1982 and on seven other occasions until December 1983.

During the 1983 burning programme in August two grids were clean-burnt (the patchy-burn grid and its adjacent clean-burn grid). Only pre-burn trapping was conducted as low rodent numbers did not justify a post-burn trapping programme.

Vegetation recovery in clean-burn 1 grid was monitored from August to December 1982. Cover

was subjectively assessed using a replicated (0.5 m²) quadrat method, which included height measured where the majority of leaves and/or inflorescences ended.

In an experiment to assess the immediate response of small mammals to the blaze, a 10 m wide fire-break was burnt around a 2.7 ha grid. The following day observers were strategically placed along the fire-break before igniting the area, in order to observe and record emigrants.

Results

Population estimates indicate that small mammal responses to the different burning treatments vary. Post-burn density on the no-burn and patchy-burn grids increased while a reduction on both clean-burn grids was evident (Table 2). The anticipated rise in numbers in the summer breeding period was stifled by the drought; population estimates showed a

Table 2. Total captures, population density estimates, diversity indexes, and trap success determined from the trapping results of four grids monitored from July 1982–Dec. 1983 in Hluhluwe Game Reserve

Grid	Year	Month	Total captured (n)	Population estimate (animals ha ⁻¹)	Diversity index	Trap success (%)
Patchy-Burn	1982	Jul	40	14.9	0.3	10.0
		Aug	35	20.9	0.3	8.8
		Sep	19	6.5	0.4	4.8
		Nov	16	6.0	0.6	4.0
	1983	Feb	8	2.6	0.7	2.0
		Apr	8	2.7	0.3	2.0
		Aug	5	2.0	0.6	1.3
		Oct	3	0.9	0	0.8
		Dec	2	0.2	0.3	0.5
Clean-Burn 1	1982	Jul	92	35.7	0.3	23.0
		Aug	38	13.7	0.2	9.5
		Sep	24	8.8	0.3	6.0
		Nov	14	5.3	0	3.5
	1983	Feb	13	5.3	0.3	3.3
		Apr	5	1.8	0.2	1.3
		Aug	9	2.8	0.3	2.3
		Oct	2	0.6	0	0.5
		Dec	2	0.9	0.3	0.5
No-Burn	1982	Jul	93	34.3	0.3	23.3
		Aug	120	43.5	0.4	30.0
		Sep	84	26.9	0.5	21.0
		Nov	43	13.3	0.5	10.8
	1983	Feb	16	5.9	0.5	4.0
		Apr	15	3.8	0.6	3.8
		Aug	2	0.4	0.3	0.5
		Oct	3	0.4	0.3	0.8
		Dec	2	0	0	0.5
Clean-Burn 2	1982	Jul	54	22.0	0.1	13.5
		Aug	49	18.6	0.1	12.3
		Sep	30	11.0	0	7.5
		Nov	14	4.4	0.2	3.5
	1983	Feb	10	2.6	0.1	2.5
		Apr	6	1.8	0	1.5
		Aug	5	2.6	0.5	1.3
		Oct	3	0.6	0.3	0.8
		Dec	4	1.8	0	1.0

Table 4. Mean range distance estimates with standard errors (SE), of four rodent species in Hluhluwe Game Reserve from July 1982 to April 1983
Differences between male and female distances are tested for significance (Student's t)

Species	n	Females distance (m)	SE	n	Males distance (m)	SE	n	Combined distance (m)	SE	t	df	p
<i>P. natalensis</i>	128	27.6	1.6	155	26.6	1.8	283	27.1	1.2	0.53	281	>0.5
<i>S. campestris</i>	1	15.0	—	1	33.5	—	2	24.3	—	—	—	—
<i>A. chrysophilus</i>	18	24.5	2.4	13	21.8	2.6	31	23.3	1.8	0.74	29	>0.4
<i>L. griselda</i>	8	19.5	3.7	19	23.0	3.5	27	22.0	2.7	0.59	25	>0.9

and post-burn comparisons were made of each grid after establishing that the age-structure in each grid did not differ significantly from the overall age-structure. A null hypothesis that the two sets of attributes, i.e. age-structure and the grid areas selected for different burning treatments, were independent of each other was upheld ($\chi^2 = 2.89$, $p > 0.8$). However, pre- and post-burn age structures of *P. natalensis* showed a significant difference in the clean-burn 2 treatment only, where the juvenile catch increased ($p < 0.05$).

Pre- and post-burn sex ratios showed no significant differences for *P. natalensis* ($\chi^2 = 0.004$, $df = 1$, $p > 0.99$), *A. chrysophilus* ($\chi^2 = 0.03$, $df = 1$, $p > 0.9$) and *L. griselda* ($\chi^2 = 2.68$, $df = 1$, $p > 0.1$). The pre- and post-burn inter-grid sex ratios of *P. natalensis* showed no significant differences ($\chi^2 = 0.0004$, $df = 1$, $p > 0.99$).

The range distance for each species is given in Table 4, *P. natalensis* appears to have a marginally greater range than *Saccostomus campestris*, *A. chrysophilus*, or *L. griselda*. Small sample sizes precluded inter-treatment analysis of range distances in all species but *P. natalensis*. Pre- and post-burn range distance fluctuations vary inversely with changes in population density estimates (Table 5).

A high percentage of pre-burn marked *P. natalensis* (75.8 and 68.1 %) and *L. griselda* (66.7 %) were caught during post-burn trapping on the clean-burn grids, while in the no-burn grid the number of pre-burn marked *P. natalensis* was relatively lower at 56.8 % with only 24.1 % of the catch in the patchy-burn grid bearing pre-burn marks. The survival rate for *P. natalensis*, *A. chrysophilus*, and *L. griselda* was highest in the no-burn treatment (Table 6).

The ratio of breeding to non-breeding *P. natalensis* decreased until November (July 1:7.1, August 1:9.7, September 1:12.5) when there was an upsurge in breeding condition and the ratio changed to 1:0.5. Analysis shows that the inter-treatment ratios vary considerably (Table 7).

The recovery of vegetation cover/height is depicted in Fig. 3; despite improved habitat conditions small mammal numbers showed a temporal decline.

Rainfall during the study period was well below average, the effect of fire, therefore, could only be investigated in the short term, i.e. before the drought had established itself.

The experiment planned to assess the small mammal response to the blaze gave no indication of animals fleeing from the flames; one of the 35 animals known to be in the area fled across the firebreak. QUINN (1979) reported burnt and unburnt carcasses of small mammals found after fires in chaparral shrubs, while TEVIS (1956) actually witnessed animals perishing in the flames. Only one unburnt carcass (*L. griselda*) was found after the fire in the experiment during the present study.

Table 5. Changes in pre- and post-burn population densities and mean range distances [with standard errors (SE) and a test for significance (Student's *t*)] of *P. natalensis* in each burning treatment

Treatment	Population density estimates (animals/ha)		Mean range distance (m)				<i>t</i>	df	<i>p</i>
	pre-burn	post-burn	pre-burn	SE	post-burn	SE			
No-burn	34.3	43.5	26.0	4.3	23.9	2.5	0.46	63	>0.5
Clean 2	22.0	18.6	24.0	3.3	24.8	2.9	0.18	40	>0.5
Patchy	14.9	20.9	20.8	4.3	16.5	1.5	0.91	19	>0.2
Clean 1	35.7	13.7	28.5	3.4	44.6	13.3	1.71	46	<0.1

Table 6. Survival rate of *P. natalensis*, *A. chrysophilus*, and *L. griselda* expressed as a percentage of the number of pre-burn marked animals caught in post-burn trapping sessions

Species	Burning treatment	Number of marked animals	Survival (%)				
			Aug	Sep	Nov	Feb	Apr
<i>P. natalensis</i>	Patchy	32	21.9	6.3	—	—	—
	Clean 1	67	37.3	17.9	9.0	—	—
	No-burn	63	73.0	38.1	19.1	3.2	—
	Clean 2	52	61.5	28.8	5.8	1.9	—
<i>A. chrysophilus</i>	Patchy	1	100.0	—	—	—	—
	Clean 1	1	—	—	—	—	—
	No-burn	3	—	—	33.3	33.3	33.3
	Clean 2	0	—	—	—	—	—
<i>L. griselda</i>	Patchy	2	—	—	—	—	—
	Clean	9	22.2	—	—	—	—
	No-burn	3	100.0	66.7	—	—	—
	Clean 2	0	—	—	—	—	—

Table 7. The ratio of breeding to non-breeding *P. natalensis* in various burning treatment areas during November 1982

Treatment	Breeding : Non-breeding		<i>n</i>
No-burn	0.9	1	17
Patchy-burn	1.5	1	5
Clean-burn 1	6.0	1	14
Clean-burn 2	4.0	1	10

Discussion

Factors influencing the rate at which burnt savanna grassland is recolonised by small mammals include behaviour of the animals involved, proximity to refugia (unburnt grassland or forest inhabited during or shortly after the blaze), rate of vegetation recovery and the type of burn. Recolonisation of burnt areas may extend between two and eight or more months and can, subsequently, yield higher small mammal numbers than unburnt areas (NEAL 1970; STEWART 1972; KERN 1977; CHEESEMAN and DELANY 1979; SWANEPOEL 1981; ROWE-ROWE and LOWRY 1982). KERN (1977), who examined the effects of annual August burns, estimated 0.62 animals/ha immediately after the fires, 2.16 animals/ha two months later, and 4.17 animals/ha in January when grasses were seeding profusely.

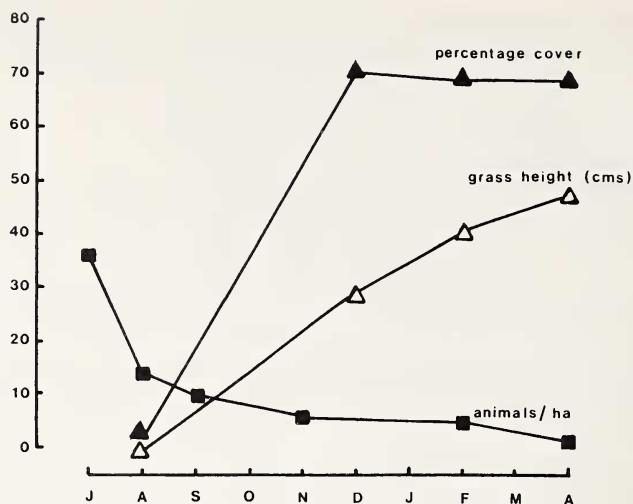


Fig. 3. Recovery of the grass sward (height and percentage cover) after an August clean-burn, related to changes in small mammal numbers, Aug 1982 to Apr 1983

The anticipated small mammal recolonisation of the burnt areas in this study did not occur despite the recovery of the herb layer, the effects of the drought are implicated.

Population estimates

Post-burn population crashes have been recorded by many workers (NEAL 1970; KERN 1977; CHRISTIAN 1977; SWANEPOEL 1981) but pre- and post-burn trapping in the present study suggest that fluctuations in small mammal numbers following fire stem mainly from dispersal. The grids providing cover (no-burn and patchy-burn) showed an increase in numbers whereas the two clean-burn grids, where all cover had been removed, exhibited decreases.

COOK (1959), however, found no evidence that surviving mice emigrated to adjacent unburnt areas, but, most studies (NEAL 1970; CHRISTIAN 1977; KERN 1981; SWANEPOEL 1981) show that migration from the burnt area to an area providing shelter is common.

Species composition

On the no-burn grid, where significant post-burn changes occurred, the number of *P. natalensis* and *L. griselda* were augmented by migrants from the surrounding burnt areas, while the rest of the community remained numerically constant. SWANEPOEL (1981) found that 25 % of *P. natalensis* migrated to an adjacent unburnt area while more mobile *L. griselda* vacated the burnt area completely. On the adjacent clean-burn 2 grid, *P. natalensis* numbers dropped by 11.3 %.

Crocidura hirta disappeared from the patchy-burn grid, while *P. natalensis* numbers increased, and *A. chrysophilus* and *L. griselda* numbers remained constant. The total post-burn captures in this grid decreased yet population estimates increased; the apparent anomaly arose from the high migration rate in this area. First, the *P. natalensis* population had been considerably diluted, only 24.1 % of the post-burn captures bore pre-burn marks compared with 56.8 % in the no-burn grid. Second, increased movement was indicated by the relatively low recapture rate of all marked animals. It is clear that the small mammal community was markedly disrupted by the patchy-burn. In the adjacent clean-